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RECEPTIVE FIELD ANALYSIS: RESPONSES TO MOVING VISUAL CONTOURS BY SINGLE LATERAL GENICULATE NEURONES IN THE CAT

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SUMMARY

1. Responses of single geniculate cells to moving light and dark bars and light/dark edges were studied in cats anaesthetized with nitrous oxide/oxygen (70 %/30 %).

2. Over 95 % (230 out of 241) of geniculate cells had antagonistic centre-surround receptive fields. Their responses could be characterized as centre-activated or centre-suppressed depending on the receptive field type (ON- or OFF-centre) and the contrast between stimulus and the background (brighter or darker than the background). Moving light and dark edges evoked responses which were very similar to the responses evoked by these stimuli in simple cells of striate cortex.

3. A number of cells (45) with antagonistic centre-surround receptive fields were classified according to their X/Y (sustained/transient) properties. Units with sustained properties (X-cells) did not increase their firing rate with an increase of stimulus velocity and some of them showed a clear-cut preference for slow movement (around 1–2°/sec). On the other hand, units with transient properties (Y-cells) showed a clear-cut preference for fast-moving stimuli (50–100°/sec.)

4. Elongation of the stimulus beyond the antagonistic surround in both X- and Y-cells produced a clear-cut reduction of amplitude of both centre and surround components of the response. Thus the existence of a suppressive field component beyond the antagonistic surround is confirmed.

5. About 5 % of cells had receptive fields which did not have an antagonistic centre-surround organization but gave a mixed ON-OFF discharge from the central region of the field. Around the central region there was a silent suppressive zone. These units were not directionally

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selective, responded preferentially to fast-moving stimuli (25–100°/sec) and had a substantial (spontaneous) maintained activity.

INTRODUCTION

The relay cells of the lateral geniculate nucleus (LGN) are directly activated by the axons of retinal ganglion cells and their axons in turn form the principal visual input to the visual cortex.

Quantitative analysis of the responses of cortical cells have been largely confined to the responses evoked by elongated moving stimuli since cortical cells respond rather poorly to stationary spots or bars (Pettigrew, Nikara & Bishop, 1968; Bishop, Coombs & Henry, 1971*a*, *b*, 1973). Therefore we undertook study of the responses of LGN cells to the elongated moving stimuli in order to distinguish those properties of cortical receptive fields which are determined by their LGN input from those of their properties which must be determined by cortical circuitry. On the other hand, comparison of our data with available analysis of the responses of retinal ganglion cells to moving elongated stimuli (Rodieck & Stone, 1965*a*, *b*) enabled us to recognize the modifications of the responses due to the neural circuitry of the LGN.

The main finding of this study is that several recently described features of the receptive fields of simple cells in the striate cortex (Bishop *et al.* 1971*a*, *b* and 1973) are determined by their input from the LGN. For example, the organization of receptive fields into discharge centres, sensitive to dark or light edges, appears to be present at the LGN, and to be determined by the centre-surround organization of LGN receptive fields.

Our additional findings support previously published results. Basic similarities are noted between the single unit responses of most LGN cells and those of retinal ganglion cells, and the existence of a 'suppressive field' in LGN receptive fields (Cleland, Dubin & Levick, 1970; Levick Cleland & Dubin, 1972) is confirmed.

METHODS

The equipment and methods used in these experiments have been described in detail by Kinston, Vadas & Bishop (1969), Joshua & Bishop (1970) and Bishop *et al.* (1971*a*). Cats (2·5–4·0 kg) were anaesthetized with ether for initial surgery and with a nitrous oxide/oxygen mixture (70%/30%) during recording. Eye movements were minimized by paralysis of striated muscles, coupled with bilateral cervical sympathectomy (Rodieck, Pettigrew, Bishop & Nikara, 1967). Paralysis was achieved by an initial I.V. injection of 80 mg gallamine triethiodide (Flaxedil; May and Baker) followed by a continuous I.V. infusion of a mixture of Flaxedil (16·2 mg/hr) and C-toxiferine I (toxiferine dichloride; Hoffmann-La Roche; 1mg/hr) in 0·9% saline

(6·5 ml./hr). Body temperature was maintained at 38° C with an electric heating blanket. The corneas were protected with zero power plastic contact lenses. The lids were retracted by Neosynephrine (2·5%) and the pupils dilated with atropine (1%). Artificial pupils (diameter 3 mm) were centred on the line passing from area centralis through the centre of the natural pupil. The modified viewing system of a fundus camera (Carl Zeiss, Oberkochen, West Germany) used for the positioning of the artificial pupils allowed also projection of retinal landmarks (blind spots, area centralis) onto a tangent screen placed at 1 m in front of the animal. Supplementary spectacle lenses were used when necessary, the appropriate power being determined by moving gratings of various spatial frequency across the receptive field of geniculate units. The lens power which enabled the unit to respond to the grating of highest spatial frequency was determined. Since, however, there was usually a range of lens power for which acuity was maximal, the lens power at mid-point was used for the rest of the experiment (cf. Cleland, Dubin & Levick, 1971*b*).

Action spikes from single LGN units were recorded extracellularly, using tungsten-in-glass micro-electrodes (Levick, 1972) and amplified in conventional manner. At the end of each experiment the brain was fixed in formalin-saline and serial histological sections through the LGN were stained with cresyl violet. In some experiments electrolytic lesions (10 μA for 10 sec) were made to facilitate identification of recording sites.

The receptive field centre of each neurone was mapped with small hand-held flashing spots of light or stationary black disks (0·1–0·5°) and the surround with large flashing spots or annuli. Only the size of the centre region was determined. As soon as the position of the central region was located small spot flashing once every second was moved sequentially toward the centre from positions above, below to the left and to the right. For each sequential movement of the spot position of the spot at which weakest clear-cut centre response could be elicited was noted and the edge of the spot nearest to the receptive field centre marked. The procedure was repeated a couple of times to ensure reproducibility of our marking. A circle or an ellipse passing through the marked points was assumed to outline the receptive field centre (cf. Hoffmann, Stone & Sherman 1972). Determination of X/*Y* (sustained/transient) properties was based on the unit's response to standing contrast, moving grating patterns and large moving spots (Cleland *et al.* 1971*b*). The usual background luminance was about 1 cd/m^2 with the stimuli 0·9–1·4 log units above the background. For quantitative analysis the magnified image of an adjustable aperture was projected onto the back of a translucent rear-projection tangent screen positioned 1 m in front of the animal. 'Light edge' stimuli were light/dark borders of positive contrast (step increase in luminance) while 'dark edge' stimuli were dark/light borders of negative contrast (step decrease in luminance). The stimuli were lined up with the centre of the receptive field and the unit's response analysed by preparing average response histograms with a specially modified RIDL Multichannel Analyser. The start of each triangular waveform signal from the function generator controlling the movement of the stimulus triggered the multichannel analyser, which then stepped on over 100 or 200 channels in synchrony with the stimulus movement in one direction and over another 100 or 200 channels as the stimulus moved in the opposite direction. Each channel therefore corresponds to a specific spatial and temporal segment of the stimulus sweep. Nerve impulses that fired during the stimulus cycle increased the count in whichever channel was open at the time of firing. The ordinate scalings of the average response histograms in this paper are in spikes/sec averaged in each case over the three channels centred on the channel containing the maximum count and the abscissae are scaled in degrees of visual angle. The points of reversal of direction of stimulus movement are indicated by the vertical arrows above each histogram.

RESULTS

We studied the receptive field properties of 241 units recorded in the LGN of forty-two cats. The majority (187) of units had receptive fields within 5° of the visual axis. Two broad classes of receptive field were found; antagonistic centre-surrounded (133 ON-centre, OFF-surround and 97 OFF-centre, ON-surround) and ON-OFF centre receptive fields (eleven units). Both classes were encountered in all laminae of the LGN and there were no apparent differences (except ocularity) between units of the same type recorded in the different laminae. The antagonistic centre-surround fields had centres ranging in diameter from 0·2 to about 3·0°, and were generally radially symmetrical, although with occasional fields the surround was apparent only on one side of the centre. Forty-five of the centre-surround units were classified according to their *X* (sustained) or *Y* (transient) properties (Enroth-Cugell & Robson, 1966; Cleland *et al.* 1971*b*; Fukada, 1971). Of the sustained units, eighteen were ON-centre units and thirteen were OFF-centre. Of the transient units nine were ON-centre units and five were OFF-centre. Mean diameter of the receptive field centre of the *X*-cells was 0·8° (0·2–1·5°) while in the *Y*-cells it was 1·8° (0·5–2·5°). The high proportion of sustained cells in our sample was probably due to the fact that they are relatively more common in that part of the LGN which receives the input from the area centralis (Hoffmann *et al.* 1972).

I. Antagonistic centre-surround receptive fields

(1) *Receptive field types: responses to narrow bars*

A. *ON-centre units.* Fig. 1 shows average response histograms obtained from three ON-centre LGN cells to light and dark bars moved across their receptive fields first in one direction (upward) and then back again (downward); the vertical arrows indicate the stimulus turn-round points. The responses of ON-centre LGN cells can be characterized as 'centre-activated' or 'centre-suppressed' (cf. retinal ganglion cells, Rodieck & Stone, 1965*a*) depending on the contrast of the stimulus. Thus, stimuli brighter than the background (light bars, Fig. 1*A*, *C*, *D*, *F*) evoked the centre-activated type of response and, conversely, centre-suppressed responses were generated by dark bars (Fig. 1*B*). The most common centre-activated response pattern (60% of cells) is illustrated in Fig. 1*A*. The first component of the response as the light bar covers the proximal part of the OFF-surround is a suppression of firing. This is followed by vigorous excitation as the stimulus crosses the ON-centre. The unit firing is once more suppressed as the stimulus crosses the surround on the far side of

the centre (distal surround). Essentially the same response pattern is observed as the stimulus crosses the receptive field in the opposite direction. The centre-suppressed responses of ON-centre units (i.e. the response evoked by a dark bar) were not studied extensively. A typical example of such a response is illustrated in Fig. 1*B*. There is a very weak discharge from the proximal part of the OFF-surround followed by a suppression of firing when the dark bar covers the ON-centre. Finally there is a strong discharge from the distal OFF-surround. The same pattern

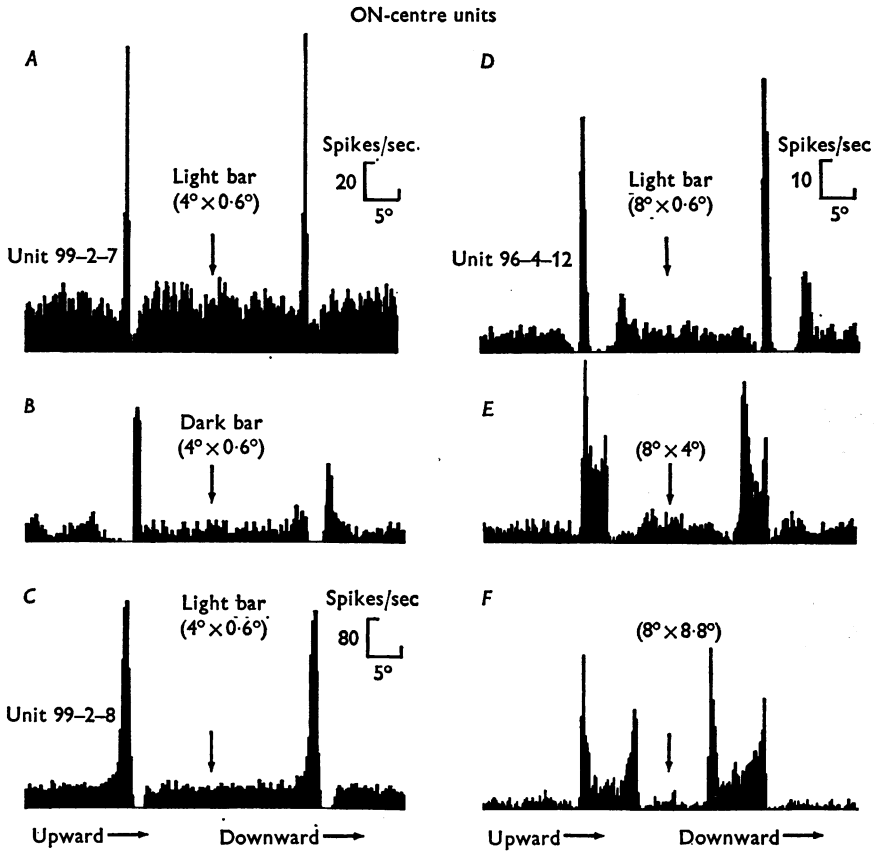

Fig. 1. Average response histograms compiled from the responses of ON-centre neurones to forty successive stimulus sweeps of a light or dark bar moving upward and downward at 5·5°/sec across their receptive fields. Histograms *A*, *C*, *D*, *E* and *F* illustrate centre-activated response patterns. Histogram *B* illustrates a centre-suppressed response pattern. The vertical arrow above each histogram indicates the point at which the stimulus reverses its direction of movement. Length (measured perpendicularly to the direction of stimulus movement) and width of the bar are indicated above each histogram.

is observed once more as the stimulus crosses the receptive field in the opposite direction.

In the remaining ON-centre units some difference in the response pattern to a light bar were observed. In about 30% of the units there was an additional discharge peak as the stimulus left the surround on the far side of the centre (Fig. 1*D*). Finally in 10% of the units there was no suppression of firing when the light bar moved into the OFF-surround in front of the centre (Fig. 1*C*). These variations in the response pattern were correlated with the relative strengths of the responses produced by centre and surround stimulation.

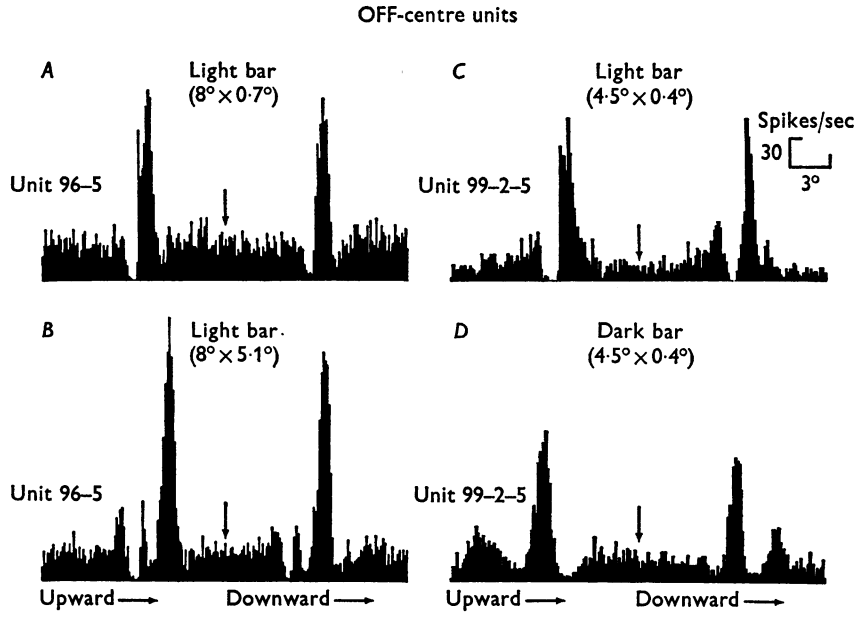

Fig. 2. Average response histograms compiled from the responses of OFF-centre neurones to forty successive stimulus sweeps of a light or dark bar moving upward and downward at 5·5°/sec across their receptive fields. Histograms *A*, *B* and *D* illustrate centre-suppressed response patterns. Histogram *D* illustrates a centre-activated response pattern. For other details see legend for Fig. 1.

B. *OFF-centre units.* Figs. 2, 4*D*, 8*C*, *F* and 9*C* show average response histograms from six OFF-centre cells to the movement of light and dark bars. These responses can also be characterized as centre-activated (Fig. 2*D*) or centre-suppressed (Figs. 2*A*, *B*, *C*, 4*D*, 8*C*, *F*, 9*C*) depending upon the contrast of the stimulus. With a narrow light bar in about 50% of

units the following phases occur in sequence (Fig. 2*A*, *C*): the cell is weakly excited as the light bar enters the ON-surround; there is strong inhibition as the bar crosses the OFF-centre; vigorous firing occurs as the bar crosses the ON-surround on the far side of centre and, finally, there is a weak suppression of firing as the bar leaves the surround. The same response pattern is obtained when the bar crosses the field in the opposite direction.

In about 25 % of OFF-centre units a narrow light bar evoked forceful discharges both from the proximal and the distal parts of the ON-surround (Figs. 8*C*, 9*C*). In the remaining 25 % of cells there was virtually no discharge from the part of the ON-surround in front of the centre and a powerful suppression of firing as the bar was leaving the distal part of the ON-surround (Fig. 8*F*). In the ON-centre units, these variations in the response patterns were correlated with the relative strength of the response produced by stimulation of centre and surround.

(2) *Responses to bars: varying stimulus parameters*

A. *Bar width.* Increasing the width of the bar always accentuates the component of the response arising from the centre of the receptive field (cf. retinal ganglion cells, Rodieck & Stone, 1965*a*). A typical centre-activated response caused by the movement of a wide light bar across the receptive field of an ON-centre unit is illustrated in Fig. 1*E* and *F*. The light edge of the bar (leading edge) suppresses the firing from the proximal part of the OFF-surround and evokes a sharp discharge from the ON-centre. This discharge peak is followed by sustained firing at a much lower level as the body of the light bar covers the ON-centre. Finally, as the dark edge of the bar (trailing edge) crosses the part of the surround on the near side of the centre, a second discharge peak rises out of the sustained firing from the centre component.

A centre-suppressed type of response due to the movement of a wide light bar over the receptive field of an OFF-centre unit is illustrated in Fig. 2*B*. There are three separate discharge peaks each of which is followed by a phase of suppression of firing. These events occur in sequence as follows: a weak discharge peak as the light edge moves over the part of the ON-surround on the near side of the centre; a powerful suppression of firing as the light edge crosses the OFF-centre; a second discharge peak as the light edge moves over the distal part of the ON-surround; a further suppression due to the presence of the body of the light bar over the OFF-centre; a third and very vigorous discharge peak as the dark edge of the bar crosses the OFF-centre, and, finally a weak, suppression as the dark edge crosses the distal part of the ON-surround.

B. *Bar length.* In all units with antagonistic centre-surround receptive fields, a very short narrow bar of the appropriate contrast produced a response which was dominated by the central component. A centre-activated response evoked by a short light bar in ON-centre cells is illustrated in the top histogram in Fig. 3*A*. As the stimulus entered the ON-centre it evoked strong excitation which was followed by inhibition as the bar left the centre and entered the distal surround, and only weak excitation as the bar left the surround. With a longer bar (1·2°) both the centre excitation and the surround excitation were enhanced. With the still

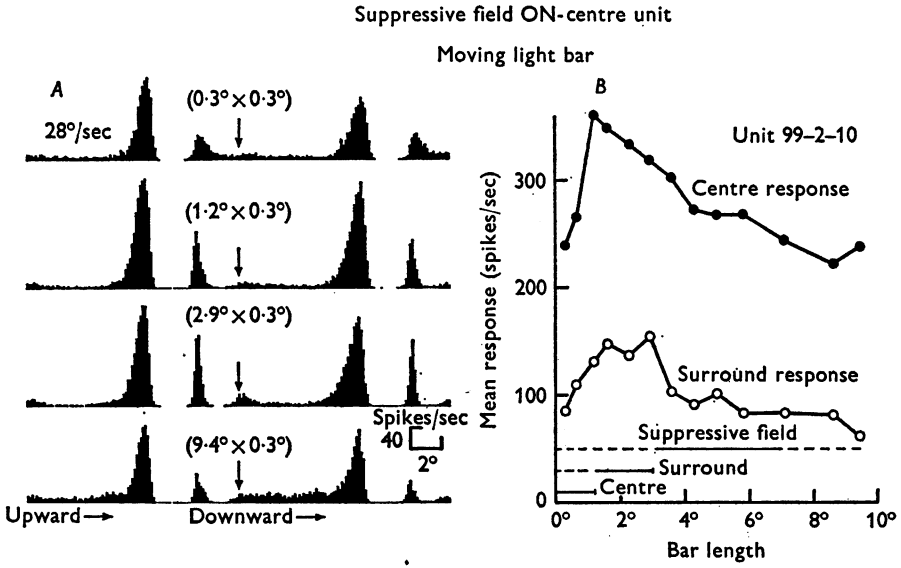

Fig. 3. Suppressive field component in LGN receptive field.

A: average response histograms compiled from the responses of an ON-centre unit to narrow (0·3°) light bars of different length moving at 28°/sec upward and downward across the receptive field. The first (larger) discharge peak in each half of every histogram is due to the response from the ON-centre of the receptive field. The second discharge peak was evoked from the distal part of the OFF-surround. For other details see legend for Fig. 1.

B: graph illustrating, for the same cell as in *A*, the relation between the length of the bar moving across the receptive field and the amplitude of the centre and the surround responses. Amplitude of the responses is expressed in spikes/sec averaged over the three channels centred on the channel containing the maximum count.

longer bar (2·9°) which extended into the receptive field surround, the amplitude of the centre excitation decreased, while the amplitude of surround excitation increased. With a 9·4° long bar, which extended beyond the antagonistic surround, both centre and surround components

of the response were reduced. This progressive reduction of both centre and surround response is ascribed to the suppressive field component described by Levick *et al.* (1972). The effect of the suppressive field can be seen more clearly in Fig. 3*B* in which the peak firing rates are plotted against bar length. The lengths of the continuous lines at the bottom of Fig. 3 represent the relative locations and spatial extents of the three

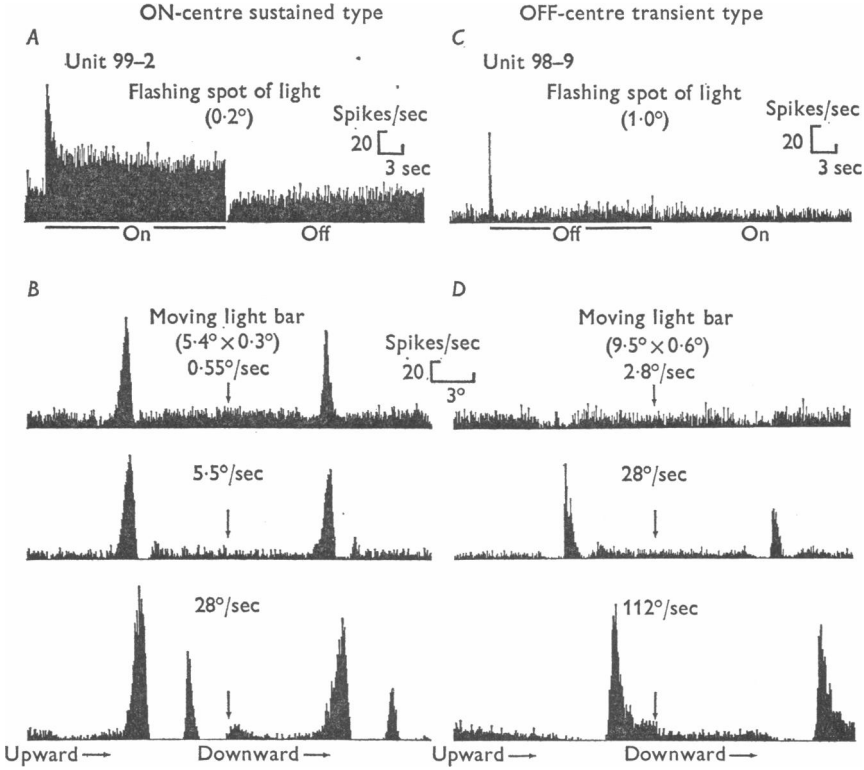

Fig. 4. *A*: average response histogram compiled from the responses of an ON-centre *X* (sustained) unit to a spot of light positioned in the centre of the receptive field and flashed on and off. The period of light on is indicated by the black line below the histogram.

B: average response histograms compiled from the responses of the same ON-centre *X* unit as in *A* to a narrow bar of light moving at different velocities (as indicated) upward and downward across the unit's receptive field. For details see text.

C: average response histogram compiled from the responses of an OFF-centre *Y* (transient) unit to a spot of light positioned in the centre of the receptive field and flashed on and off. The period of light off is indicated by the black line below the histogram.

D: average response histograms compiled from the responses of the same OFF-centre *Y* cell as in *C* to a narrow light bar moving at different velocities (as indicated) upward and downward across the unit's receptive field.

receptive field components: centre, surround and suppressive field. The amplitude of the centre response was maximal when the bar was 1·2° long, at which time it spanned the whole of the ON-centre of the receptive field, and the centre responses decreased markedly as the length of the bar was increased up to 4·3°. With still further increase in bar length, the amplitude of the centre response decreased more gradually, falling to about 70% of the maximal amplitude when the bar was 9·4° long. The

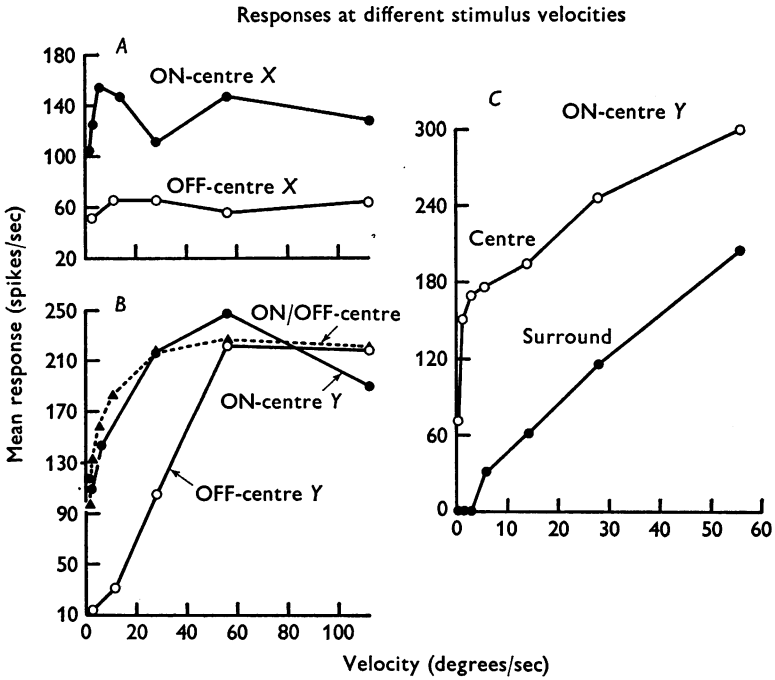

Fig. 5. Graphs illustrating the relationship between the velocity of a narrow (0·3°) light bar moving across the receptive field of various LGN cells and the amplitude of the responses either from the centre component (*A* and *B*) or from both the centre and surround components (*C*). The various cells were as follows. *A*: two *X* cells, one ON-centre and the other OFF-centre. *B*: two *Y* cells, one ON-centre and the other OFF-centre and an ON/OFF centre cell. *C*: an ON-centre *Y* cell.

amplitude of the surround response increased rapidly up to a bar length of 2·4° and thereafter decreased at first rapidly until the bar length was 5°, after which further lengthening failed to modify the amplitude of the response. The suppressive field was purely inhibitory and did not evoke any discharge peaks in the average response histogram. A silent suppressive field component was found to be present in both *X*- and *Y*-LGN cells.

C. Bar velocity. In general LGN neurones respond to moving stimuli over a wide range of velocities. There were, however, characteristic velocity-dependent changes in the pattern of their responses. Thus, in the centre-activated type of response, in both ON-centre and OFF-centre units, there is very little excitation as a slowly moving stimulus (less than 2–5°/sec. leaves the surround on the far side of the centre (Figs. 4*B* and 5*C*). When the stimuli were moved at higher velocities (20–60°/sec), however, the discharge from the distal surround was, in many units, much more vigorous (Figs. 4*B* and 5*C*). In the centre-suppressed types of response, slowly moving stimuli usually evoked a clear-cut suppression of firing as the stimulus left the surround on the far side of the centre. This suppression was not present when the stimuli moved at velocities above 50°/sec (Fig. 4*D*, bottom histogram).

We found clear-cut differences between the response/velocity functions of *X*- and *Y*-units with sustained properties (e.g. Fig. 4*A*, *B*) discharged vigorously to slowly moving elongated stimuli, and increasing stimulus velocity did not produce a clear-cut increase in response amplitude (Figs. 4*B* and 5*A*). Numerous *X*-units with receptive fields close to the area centralis had very small centres (0·2–0·4°) and did not respond at all to stimuli moving faster than 3–5°/sec. By contrast, *Y*-(transient) cells (Fig. 4*C*, *D*) responded rather weakly or not at all to slowly moving elongated stimuli and discharged vigorously at velocities of 50–100°/sec (Fig. 5*B*).

(3) *Responses to single light and dark edges*

Nearly all LGN neurones respond vigorously to both light edges (step increase in luminance) and dark edges (step decrease in luminance). When a single edge is moved over the receptive field in one direction and then back over the field in the opposite direction it leads to a reversal of stimulus contrast in relation to the direction of movement. Thus in Fig. 6, for example, a light edge (L) on the upward sweep necessarily became a dark edge (D) on the downward sweep, the first half of the average response histogram being to one type of edge and the second half to the other type. This reversal of contrast is illustrated in another way in Fig. 6 *A* and *B*: in *A* it was the light edge that was used for the upward sweep whereas in *B* it was the dark edge, the starting position for the two edges being the same in each case. The two histograms, *A* and *B*, are mirror images. A similar pattern is shown for another type of ON-centre cell in Fig. 6*D*, *E*.

A. *On-centre cells.* In the majority of ON-centre cells (20/37 tested; Figs. 6*A* and 7*A*) the light edge (L) generated a sharp burst of firing as it crossed the ON-centre and produced periods of suppression of the maintained discharge as it crossed the OFF-surround on either side of the

centre (Fig. 6*A*, upward). The same response pattern was observed when the direction of stimulus movement was reversed (Fig. 6*B*, downward). Conversely, the dark edge (D) irrespective of the direction of movement, suppressed the cell's firing as it crossed the ON-centre and generated peaks

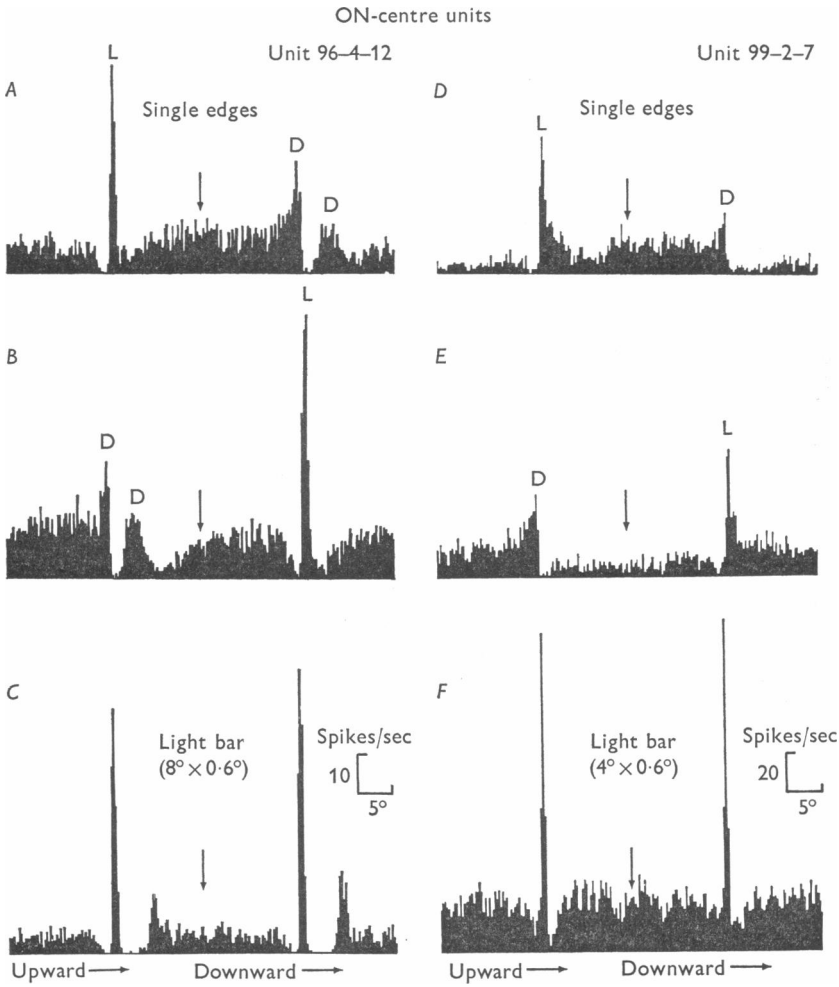

Fig. 6. Average response histograms compiled from the responses of two ON-centre cells to light (L) and dark (D) edges and narrow light bars moving at 5·5°/sec upward and downward across their receptive fields. For details see text and legend for Fig. 1.

of firing as it crossed the surround on either side of the centre (Fig. 6*A*, downward and Fig. 6*B*, upward). The discharge evoked by the dark edge from the OFF-surround on the far side of the centre was less vigorous

than the dark edge discharge from the OFF-surround on the near side. For a narrow light bar these cells fired maximally when the light edge of the bar crossed the ON-centre region at the same time as the dark edge of the

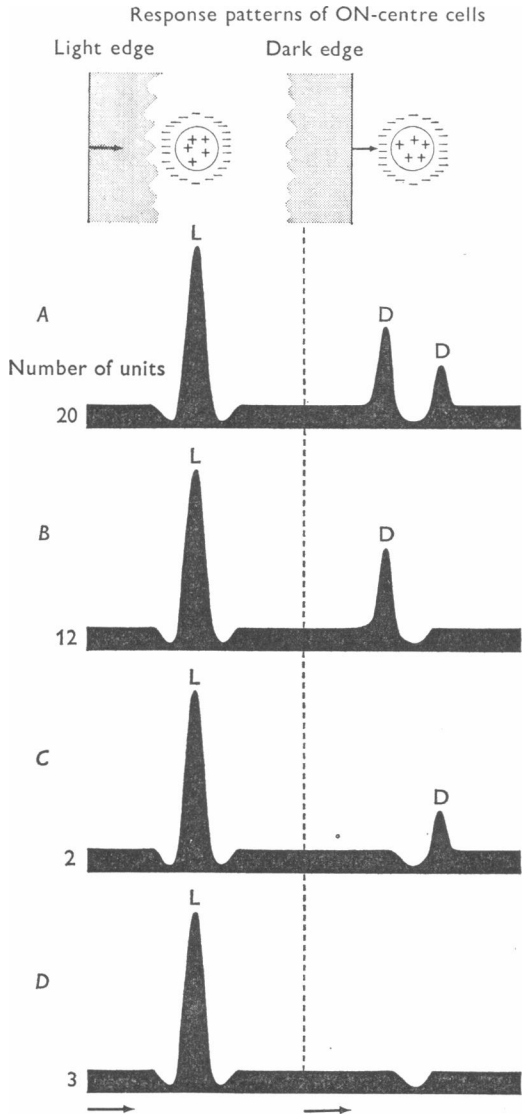

Fig. 7. Schematic diagrams of the four types of response patterns of ON-centre LGN units to moving single light (L) and dark (D) edges. The left halves of the diagrams illustrate the responses to the light edges while the right halves illustrate the responses to the dark edges. Only one direction of movement is illustrated since the responses were virtually identical for all directions of movement. For details see text.

bar crossed the surround. Thus the discharge peak evoked by a narrow bar falls between the discharge peaks evoked by the single light and dark edges (Fig. 6*C*).

In another twelve ON-centre unit (Figs. 6*D*, *E* and 7*B*) the response pattern to the light edge did not differ from that described above. Irrespective of direction of movement the light edge suppressed the cell's firing when it passed through the OFF-surround on the near side of the centre and evoked a burst of firing from the ON-centre itself (Fig. 6*D*, upward and Fig. 6*E*, downward). The dark edge, however, unlike in the cells described above caused only a rather small discharge peak as it crossed the part of the OFF-surround on the near side of the ON-centre. Again the discharge peak evoked by a narrow bar falls between the dark and light edge discharge peaks (Fig. 6*F*).

The other two types of ON-centre cell responses to single edges were relatively uncommon (Fig. 7*C*, *D*). In two cells the response pattern to the light edge was once more the same as in Fig. 7*A*, but the dark edge evoked discharges only from the part of the OFF-surround on the far side of the centre (Fig. 7*C*, dark edge). Finally, in three cells, the response pattern caused by the light edge was the same as from other ON-centre units but the dark edge caused only suppression of the firing as it crossed the ON-centre without evoking any discharge from the OFF-surround (Fig. 7*D*).

In all types of ON-centre/units, dark edges evoke much less vigorous firing than the light edges. When the discharge centre analysis proposed for cortical receptive fields by Bishop *et al.* (1971*a*) is applied to the LGN units it indicates that 'discharge centres' for light and dark edges are offset with respect to one another. In Type A ON-centre units (Figs. 6*A*, *B*, *C* and 7*A*) the dark edge discharge centres, irrespective of direction of stimulus movement, lie on both sides of the light edge discharge centre. In Type *B* units (Figs. 6*D*, *E*, *F* and 7*B*) the dark edge discharge centre for both directions of movement lies nearer the starting-point of stimulus movement than the light edge discharge centre. As the direction of stimulus movement is reversed the position of the light edge discharge peak remains approximately the same while the dark edge discharge centre is shifted to the other side of the light edge centre. The separation of light and dark edge discharge centres is approximately equal to the distance between the maximally sensitive regions of the centre and the part of the surround on the near side of the centre. In Type *C* (Fig. 7*C*) units the dark edge discharge centre, irrespective of direction of stimulus movement, lies further away from the starting-point of stimulus movement than the light edge discharge centre. In Type *D* units (Fig. 7*D*) there is only a light edge discharge centre.

B. *OFF-centre cells.* The response patterns to single edges by OFF-

centre cells are nearly mirror images of those from ON-centre cells to the same stimuli. Two common types of response patterns are illustrated in Fig. 8 and once again, as in Fig. 6, there has been a reversal of stimulus contrast at the beginning of the sweep in Fig. 8*A* and *B* and again in Fig. 8*D* and *E*.

Ten out of twenty-six OFF-centre units responded to the dark edge with a vigorous discharge from the centre and a weak suppression of firing from the ON-surround on one or both sides of the centre (Figs. 8*A*, *B* and 10*A*, dark edge). The light edge generated two peaks of firing from the

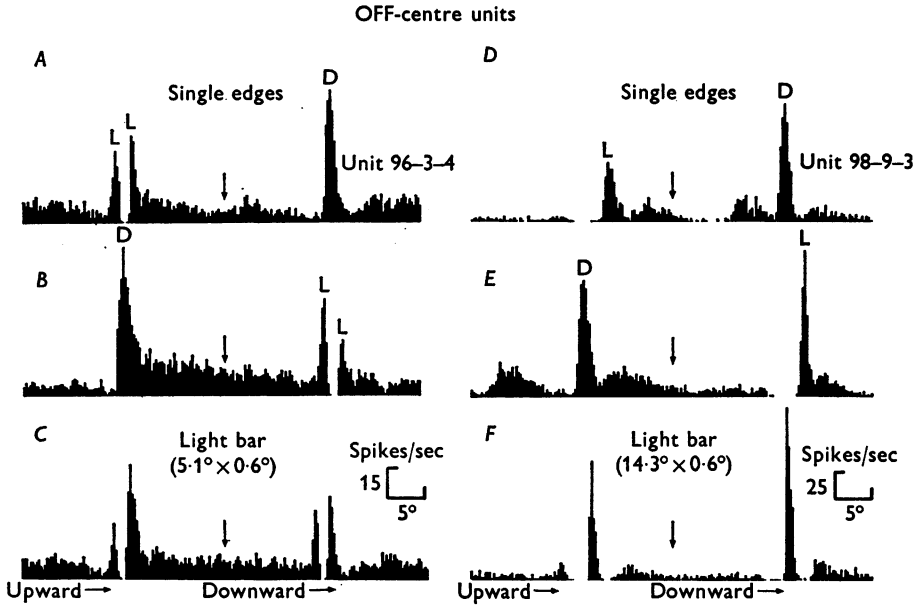

Fig. 8. Average response histograms compiled from the responses of two OFF-centre LGN cells to light (L) and dark (D) edges and narrow light bars moving at 5·5°/sec upward and downward across their receptive fields. For details see text.

surround, one from the near side and one from the far side of the centre and caused a suppression of firing while crossing the centre (Figs. 8*A*, and 10*AB*, light edge). A narrow bar caused discharges from the ON-surrounds on either side of the centre (double peak in Fig. 8*C*).

Seven cells gave responses like those illustrated in Figs. 9 and 10*B*. A light edge evoked a discharge as it crossed the near side of the ON-surround and slightly depressed the cell's firing as it crossed the centre. A dark edge, conversely, suppressed firing from the near side of the ON-surround, and excited the cell from the centre region. In the terminology

proposed by Bishop *et al.* (1971*a*) these cells would thus have offset discharge centres, the light edge discharge centre being nearer the starting point of the stimulus movement than the dark edge discharge centre. In six of these seven units a narrow light bar evoked a response pattern with two discharge peaks (Fig. 9*C*). One peak of firing is elicited as the narrow bar crosses the ON-surround on the near side of the centre, the second peak coincides with its exit from the OFF-centre.

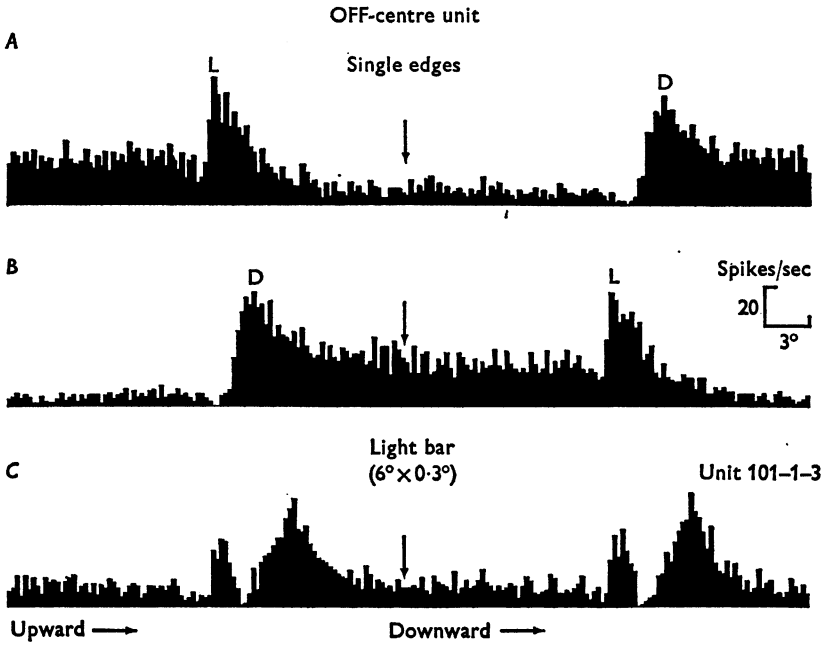

Fig. 9. Average response histograms compiled from the responses of an OFF-centre cell to light (L) and dark (D) edges and to a narrow bar of light moving at 5·5°/sec upward and downward across the unit's receptive field. For details see text.

In six other OFF-centre cells, single edges crossing the receptive field caused responses similar to the responses illustrated in Figs. 8*D*, *E*, *F* and 10*C*. A light edge stimulus suppressed the cell's firing from the OFF-centre and evoked a discharge only from the ON-surround on the far side of the centre (Fig. 8*D*, upward; Fig. 8*E*, downward). The dark edge crossing the ON-surround on either side of the centre suppressed the unit's firing and evoked a vigorous discharge from the OFF-centre (Fig. 8*D*, downward; Fig. 8*E*, upward). These cells, therefore, resemble ON-centre cells in that the dark edge discharge centre appears nearer to the starting-point of movement than the light edge discharge centre. They differ,

however, from ON-centre cells in that the dark edge discharge was generally stronger than the light edge discharge. They differ also from the apparently similar type of ON-centre cell (Fig. 7*B*) because, with reversal of the direction of stimulus movement, the spatial location of the dark edge discharge peak remains approximately the same while the light edge discharge

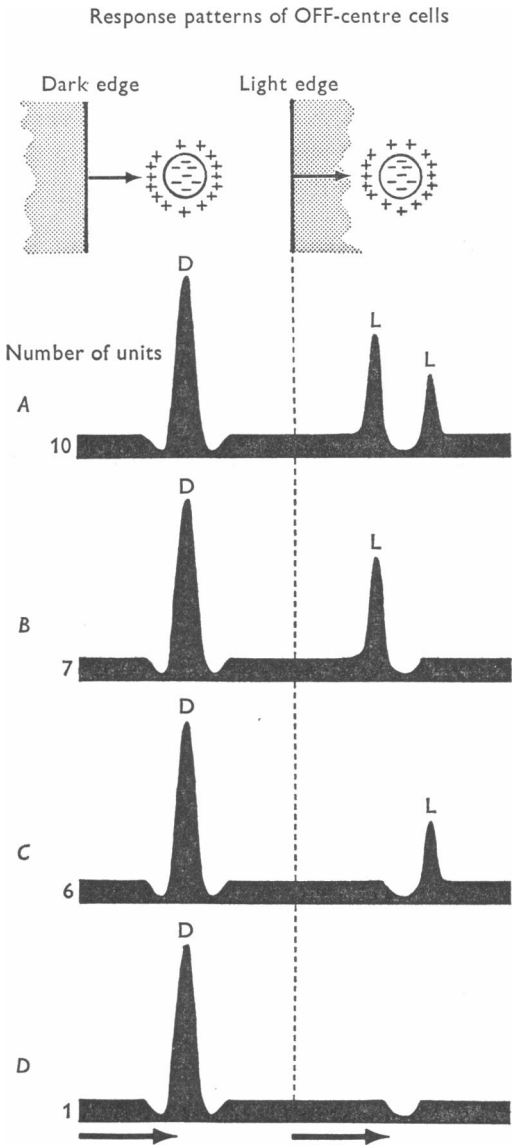

Fig. 10. Schematic diagrams of the four main types of response patterns of OFF-centre cells to moving single edges. For details see legend for Fig. 7.

centre is shifted to the other side of the dark edge centre. Finally, the two types of cell, ON-centre and OFF-centre, differ in that the separation of the discharge peaks is significantly greater in the case of the OFF-centre cells. Specifically, for receptive fields with ON-centre regions 0·3–0·5° in diameter, the mean separation of light and dark edge discharge peaks was 1·1° (range 0·7–1·4°), while for OFF-centre units of the same centre size the mean separation was 1·6° (range 1·4–1·8°). In these OFF-centre cells, as in ON-centre cells, a narrow moving light bar evokes a single discharge peak. The peak reaches a maximum when the light edge of the bar is crossing the surround on the far side of the centre at the same time as the dark edge is crossing the centre region. Consequently, the narrow bar discharge peak falls between the light and dark edge peaks, as in ON-centre cells.

In one OFF-centre cell the dark edge generated a discharge from the centre, and suppressed the cell's firing when passing through the surround on either side of the centre (Fig. 10*D*, dark edge). The light edge did not evoke any discharge and suppressed the cell's firing when crossing the OFF-centre (Fig. 10*D*, light edge).

In two OFF-centre cells not included in Fig. 10, an excitatory response was evoked only by narrow dark bars. Light and dark edges, and light bars, caused only suppression of firing.

Latencies of the responses to single edges

The latencies of the discharges to moving stimuli were assessed by the velocity method (Bishop *et al.* 1971*a*) in six ON-centre and five OFF-centre units. It varied from unit to unit ranging from 33 to 58 msec. When the light and dark edges of a bar were 1·5–2·0° or more apart, the latencies of the responses evoked by the two edges were very similar in any one unit. However, for narrow bars less than 1·5–2·0° across, the proximity of the two edges caused a delay in the response to the trailing edge of the bar (dark edge in the case of light bars, light edge in the case of dark bars). A similar increase in the latency of the trailing edge discharge has also been observed when simple cells of visual cortex are stimulated by narrow bars (Bishop *et al.* 1971*a*).

II. ON/OFF-centre receptive fields

Eleven cells (over 4% of the total population) gave brief, transient bursts of ON/OFF firing when a small spot of light was flashed anywhere within the central excitatory region of their receptive field (Fig. 11). Moving light and dark objects also caused discharges from all over the central region. Responses to moving stimuli were not directionally selective. The cells had a substantial spontaneous activity (5–50 spikes/sec: Fig. 11)

and were particularly responsive at stimulus velocities in the range 25–100°/sec (Fig. 6*B*) (cf. Kozak, Rodieck & Bishop, 1965). The diameter of the discharge areas varied from 0·8 to 1·7° (mean 1·2°). Elongation of the stimulus produced initially an increase in the discharge amplitude, presumably due to summation of excitation (Fig. 11*B*) but further elongation reduced the amplitude of the response (Fig. 11*C*), suggesting the presence of an inhibitory surround.

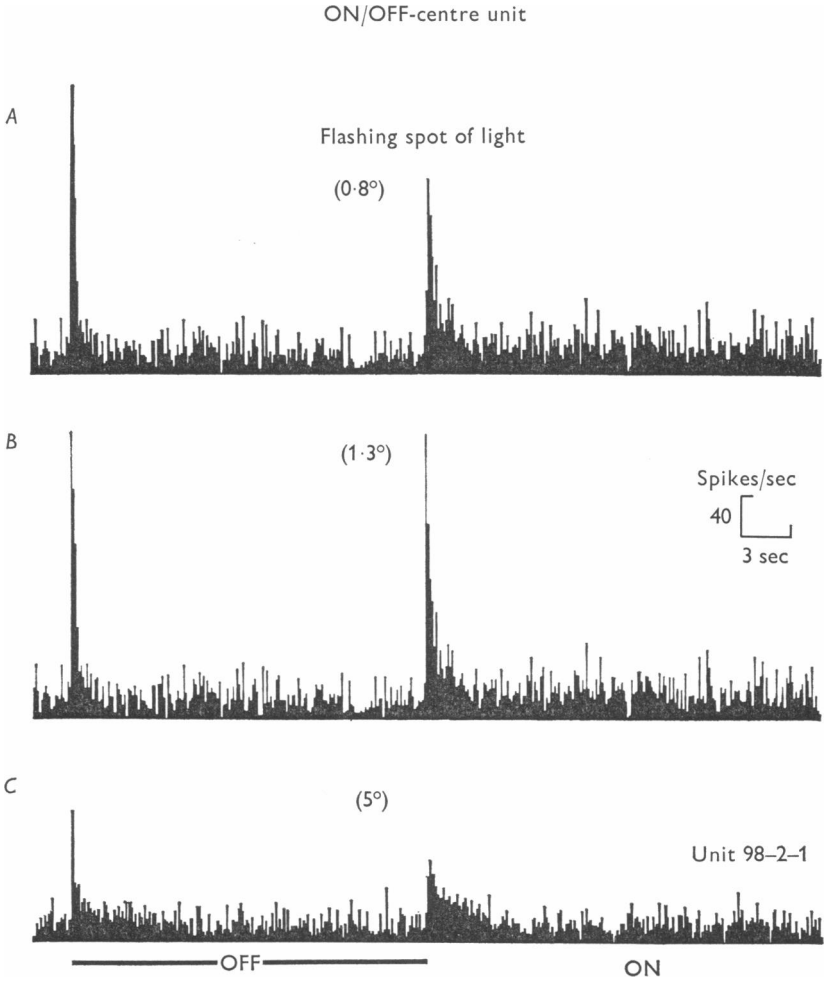

Fig. 11. Average response histograms compiled from the responses of an ON/OFF centre cell to spots of light of different diameter (as indicated above each histogram) positioned in the centre of the unit's receptive field and flashed on and off. For details see text.

DISCUSSION

A. *Similarities between LGN and retinal responses*

Anatomical studies of cat's LGN reveal a nucleus of fairly complex organization (Peters & Palay, 1966; Szentágothai, Hámori & Tömböl, 1966; Famiglietti 1970; Guillery & Scott, 1971). However, there is a striking similarity between responses of LGN cells with the concentrically organized receptive fields and responses of retinal ganglion cells as described by Rodieck & Stone (1965*a*, *b*). In particular, in both cases, responses can be described as 'centre-activated' or 'centre-suppressed', depending on the receptive field type (ON- or OFF-centre) and on the contrast of the stimulus (brighter or darker than the background). Furthermore, increasing the width of the stimulus produces in both retinal ganglion cells and LGN cells enhancement of the central component of the response.

The similarity of the response patterns of retinal ganglion cells and LGN cells supports conclusions reached by previous workers (Bishop *et al.* 1958; Hubel & Wiesel, 1961; Fuster, Creutzfeldt & Straschill, 1965; McIlwain & Creutzfeldt, 1967; Cleland *et al.* 1971*a*) that LGN cells receive an excitatory drive from one or only a few retinal ganglion cells of the same type (ON-centre or OFF-centre).

B. *Differences between LGN and retinal responses*

There are some properties of LGN cells which can only be explained as the result of an intra-geniculate neural network. One of them is the suppressive field component described for the first time by Cleland *et al.* (1970). McIlwain & Creutzfeldt (1967), during quasi-intracellular recording from ON-centre LGN units, observed hyperpolarizing potentials superimposed on depolarizing potentials whenever either a centrally positioned small spot of light or a light annulus covering OFF-surround were flashed on or off. Levick *et al.* (1972) suggested, on the basis of the McIlwain & Creutzfeldt observations, that 'the suppressive field is not merely, a remote annular zone but would be present right to the centre'. The suppressive field has only a relatively weak effect on the responses evoked by narrow bar and single edges both from the receptive field centre and the surround (Fig. 3). On the other hand, Cleland *et al.* (1970) report that coarse gratings moved in the far surround of the receptive field of LGN cells (4° from the centre) can 'suppress completely the response of a unit to a flashing spot in its centre or a flashing annulus in its antagonistic surround'.

Analogously, during eye movements, the retinal image of a contoured visual environment moved across the retina may generate significant

suppression of the responses of LGN cells. Suppression of firing during eye movements was actually observed in LGN cells of the rat (Montero & Robles, 1971). Another physiological effect, which is probably mediated by interneurones whose axons cross from one geniculate cell layer to another, is the presence in an overwhelming majority of LGN units (in addition to the normal receptive field in the dominant eye) of a purely inhibitory receptive field in the homonymous hemifield of the non-dominant eye (Sanderson, Darian-Smith & Bishop, 1969; Sanderson, Bishop & Darian-Smith, 1971; Singer, 1970). These inhibitory receptive fields are present in both *X* and *Y* LGN cells (K. J. Sanderson & B. Dreher, unpublished observations).

It seems unlikely that the LGN cells with ON/OFF centre receptive fields are driven by the ON/OFF centre retinal ganglion cells described by Stone & Fabian (1966) and Stone & Hoffmann (1972). The LGN cells have considerable spontaneous activity and respond well to high velocity movements whereas retinal ON/OFF cells have a very low rate of spontaneous firing and are generally unresponsive to stimuli moving at more than 30–50°/sec. There is also considerable evidence that retinal ON/OFF centre cells project to the superior colliculus rather than to the LGN (Hoffmann, 1972). It seems more likely that the ON/OFF centre LGN cells are I-cells (interneurones; Type A short axon cells of Tömböl, 1969) receiving input either by recurrent collaterals from both ON-centre and OFF-centre principal (relay or P) LGN cells (Burke & Sefton, 1966; Singer & Creutzfeldt, 1970; Cleland *et al.* 1971*b*) or directly from ON-centre and OFF-centre retinal ganglion cells (Singer & Creutzfeldt 1970). I-cells in turn inhibit the P-cells and thus form the anatomical basis of the suppressive field component.

C. *Similarities between LGN and cortical responses*

Despite the virtual lack of spontaneous (maintained) activity in the simple cells of the striate cortex, at least in cats anaesthetized with nitrous oxide/oxygen (Pettigrew *et al.* 1968; Bishop *et al.* 1971*a*, 1973) there is a striking similarity between their response patterns to moving stimuli and the response patterns of geniculate cells with antagonistic centre-surround receptive fields.

Both cortical and geniculate receptive fields can be subdivided into spatially-offset edge-specific discharge centres (Bishop *et al.* 1971*a*, *b*, 1973). In 50% of the simple cells described by Bishop *et al.* (1971*a*), with elongated stimuli moving along an axis perpendicular to the optimal orientation, the spatial arrangement of the light edge and dark edge discharge centres resembled the spatial arrangement found by us in Type B ON-centre geniculate cells (Fig. 7*B*) and Type C OFF-centre cells

(Fig. 10*C*). Specifically, the dark edge discharge centre was positioned closer to the starting point of stimulus movement than the light edge discharge centre, irrespective of the direction of stimulus movement. Furthermore, in both simple and geniculate cells, a narrow light bar evoked a discharge from the region between the dark and light edge discharge centres.

In 35% of the simple cells in the sample described by Bishop and his colleagues, the light edge discharge centre lay closer to the starting-point of stimulus movement than the dark edge centre. A similar spatial arrangement was observed in Type C ON-centre (Fig. 8*C*) and Type B OFF-centre (Fig. 10*B*) geniculate cells. Interestingly, in many simple cells with such a spatial arrangement of light and dark edge discharge centres, a narrow light bar evoked two discharge peaks from completely spatially separate regions ('bimodal cells'; Pettigrew *et al.* 1968; Bishop *et al.* 1971*a*). Similarly, in the majority of Type B OFF-centre geniculate cells, narrow light bars evoked two spatially offset discharge peaks. Furthermore, some multimodal simple cells (cf. Fig. 11*B* in Bishop *et al.* 1971*a*) had similar spatial arrangements of discharge centres as Type A ON-centre geniculate cells (Fig. 8*A*). Finally, in many simple cells, a narrow bar evokes additional discharge peaks (the excitatory flanks of Bishop *et al.* 1971*c*) when the stimulus velocity was increased to about 20°/sec. This additional peak probably corresponds to the vigorous discharge evoked at higher stimulus velocities from the surround of the geniculate cells (Figs. 5*B* and 6*C*).

From the above-mentioned similarities two important conclusions can be drawn: the first is that the discharge centre organization of simple cells described by Bishop *et al.* (1971*a*, *b* and 1973) is a property of the geniculate input to these cells; the second is that cortical simple cells receive a direct excitatory input from either ON-centre or OFF-centre LGN cells but not from both. The properties of the geniculate input do not, however, explain such properties of the cortical receptive field as orientation specificity and direction selectively. These properties must be determined by cortical circuitry.

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